Copulation calls in female chimpanzees (Pan troglodytes schweinfurthii) convey identity but do not accurately reflect fertility

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Copulation Calls in Female Chimpanzees (*Pan troglodytes schweinfurthii*) Convey Identity but Do Not Accurately Reflect Fertility

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Abstract Copulation calls are a relatively common feature of female primate behavior thought to function in the advertisement of female receptivity and subsequent incitation of male–male competition. To date, the majority of work on copulation calling behavior has focused on various monkey species, with little empirical evidence from the great apes. Previous research on wild chimpanzees (*Pan troglodytes schweinfurthii*) has suggested that estrous females produce copulation calls to avoid monopolization by single males and to minimize competition from other females. We here extended these findings by investigating to what degree these social demands were reflected in the calls' acoustic structure. We recorded and acoustically analyzed 71 copulation call bouts from 6 adult female chimpanzees in the Budongo Forest, Uganda. We did not find any acoustic differences in calls given by females in fertile and nonfertile periods, as assessed by their hormonal profiles. However, the calls' acoustic structure did reliably encode identity cues of the calling female. We propose that, in chimpanzees, the use and morphology of copulation calls have jointly been shaped by the selective advantage of concealing fertility. Owing to the low visibility conditions associated with chimpanzees' natural forest habitat and their dispersed social system, providing identity cues may be of particular biological relevance for these nonhuman primates.

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Keywords Acoustic structure · Chimpanzees · Female–female competition · Information content

Introduction

A number of social mammals are known to produce vocalizations during mating, including African elephants (*Loxodonta africana*: Poole *et al.* 1988), elephant seals (*Mirounga angustirostris*: Cox and LeBoeuf 1977) and various primates, e.g., *Homo sapiens* (Dixson 1998; Hamilton and Arrowood 1978). Because of their distinct acoustic features and potential fitness consequences, considerable debate has surrounded the function of these signals, especially in primates. Explanations for their pervasiveness range from calls being mere incidental by-products of the copulatory act to calls synchronizing orgasm between mating partners (Hamilton and Arrowood 1978). To date, *ca.* 14 different hypotheses have been put forward, all of which share a common theme: copulation calls are sexually selected traits that benefit the calling female's reproductive success (Pradhan *et al.* 2006). Despite the wide range of theories, more traditional male-competition-based explanations are often preferably invoked.

One influential hypothesis is that copulation calls in females have evolved to alert nearby males to the female's receptive state, inciting direct competition between males via copulation interference so that the female mates with the most dominant and genetically superior male (Nikitopoulos *et al.* 2004; O'Connell and Cowlishaw 1994; Oda and Masataka 1995; Semple 1998). However, support for this theory with regard to primates is limited. In chacma baboons (*Papio ursinus*), no clear evidence links copulation calling with aggressive interactions (O'Connell and Cowlishaw 1994) whereas in Japanese macaques (*Macaca fuscata*) the opposite pattern was found: copulations were interrupted aggressively albeit in the absence of copulation calls (Nikitopoulos *et al.* 2004; Oda and Masataka 1995).

Male–male competition can also occur indirectly. This is the case if copulation calls incite multiple males to mate with the calling female, thus providing a platform for scramble competition between the males' sperm, a theory for which there is empirical support. For example, in Barbary macaques (*Macaca sylvanus*) the time interval between successive copulations is significantly shorter if a mating event is accompanied by copulation calls than without (Semple 1998). Subtle changes in the calls' acoustic structure may play an additional role. In yellow baboons (*Papio cynocephalus ursinus*), copulation calls encode the identity of the female and the rank of the male mating partner (Semple 2001; Semple *et al.* 2002). In Barbary macaques, the probability of ejaculation is conveyed, while the time of ovulation and hence the fertility of the female is concealed (Pfefferle *et al.* 2008). In both species, such information potentially allows males to make informed decisions regarding the identity of the female and whether interference is likely to be beneficial and successful (Pfefferle *et al.* 2008; Semple 2001; Semple *et al.* 2002). For females, inciting sperm competition and concealing ovulation is advantageous because it provides access to sperm from the most competitive and hence genetically superior males (Henzi 1996; O'Connell and Cowlishaw 1994). Mating with multiple males is also beneficial because it may secure the future survival of offspring through paternity confusion and infanticide prevention (Pradhan *et al.* 2006; van Schaik 2000).

In their natural forest habitat, chimpanzees live in fission–fusion groups, i.e., individuals typically split up and travel in small parties of less than a dozen individuals, and the composition of these parties can change throughout the day (Boesch and Boesch Achermann 2000; Goodall 1986). As a consequence of this social system and the dense nature of the forests they inhabit, males do not always have direct visual contact with females, which makes it difficult for males to track changes in female reproductive state and social relations. Therefore, copulation calls may play a crucial role, providing other group members with potentially important contextual and acoustical information for future behavioral decisions. In previous research we posited that female chimpanzees use copulation calls strategically to maximize paternity confusion among males and reduce intragroup female–female competition (Townsend *et al.* 2008). By focusing on the contexts in which copulation calls were produced, we found that calling behavior did not correlate with proximity to ovulation, but there were effects of audience presence: females specifically called less in the presence of higher-ranking females when mating with high-ranked males. Although initially dismissed (De Waal 1982), it is now becoming increasingly clear that female competition over food or potential mates is an important feature of female chimpanzee social life (Emery Thompson *et al.* 2008; Kahlenberg 2006; Kahlenberg *et al.* 2008a, b; Murray *et al.* 2007; Pusey et al. 1997) and this threat seems to be reflected by changes not only in their social behavior, but also in their vocal behavior. Avoiding ovulation advertisement with copulation calls is likely to prevent monopolization by the most powerful male and thereby reduce the infanticidal tendencies of males that have been able to copulate successfully, while the ability to inhibit copulation calls strategically allows females to mitigate the risks associated with female competition over males (Townsend *et al.* 2007, 2008). Our previous research, however, did not take into account differences in the fine acoustic structure of chimpanzee copulation calls. As acoustic variation plays a crucial role in the overall understanding of the adaptive function of copulation calls, we were interested to investigate whether the production and structure of copulation calls have been shaped by similar selective forces.

We analyzed the acoustic structure of copulation calls produced by 6 adult female chimpanzees of the Sonso community in the Budongo Forest, Uganda. If the paternity confusion function holds, then we predicted that there would be no acoustic differences in copulation calls given by a female during her fertile ovulatory phase and during a nonfertile period, e.g., the postovulatory period, when conception is impossible (Pfefferle *et al.* 2008). Second, we predicted that calls should be easily assignable to individuals because female chimpanzees have individualized relationships with males (Muller *et al.* 2006), live in visually dense habitat, and tend to overlap in their ovarian cycles (Goodall 1986).

Methods

Study Site and Subjects

We studied the Sonso community of the Budongo Forest, Uganda, in January–April 2006 and October 2006–March 2007. Over this period, we observed 287

copulations, during which females produced calls on 104 occasions. Copulation calls in female chimpanzees consist of a rhythmic succession of high-frequency, low-amplitude squeaks (Fig. 1), typically following male intromission. We recorded 71 high signal-to-noise ratio call bouts from 6 adult cycling females using all-day focal follows throughout the female's maximum tumescence phase. We determined maximum tumescence following Furuichi's (1987) method, which uses degree of wrinkling of the sexual swelling (on a 4-point scale at Budongo) as the main parameter. If >1 female was maximally swollen, we in addition recorded copulation calls *ad libitum*.

Urine Sample Collection, Hormone Analysis, and Assessment of Fertile Period

To determine approximate timing of ovulation, we collected regular urine samples during the period of maximum tumescence, with sampling gaps of ≤2 d (mean±SEM: 0.28±0.08). We collected samples directly after an individual had urinated by aspiration of the urine from plastic sheets or vegetation using disposable plastic pipettes. We analyzed samples for immunoreactive pregnanediol glucuronide (PdG), using enzyme immunoassay procedures (Townsend *et al.* 2008). The sensitivity of the assay at 90% binding was 12.5 pg. Serial dilutions of urine samples of the follicular and luteal phase gave displacement curves parallel to those obtained with the appropriate standard. Intra- and interassay coefficients of variation, calculated from replicate determinations of quality controls, were 7.94 and 6.52% (high) and 13.31 and 11.26% (low), respectively. To compensate for variations in the volume and concentration of urine samples, we divided all hormone levels by the urinary creatinine concentration as described in Bahr *et al.* (2000). Based on the defined postovulatory rise in PdG levels, the day of ovulation was presumed as the day preceding the day of PdG increase (Deschner *et al.* 2003, 2004). Based on human data regarding the survival time of ovum and sperm, we defined the fertile period

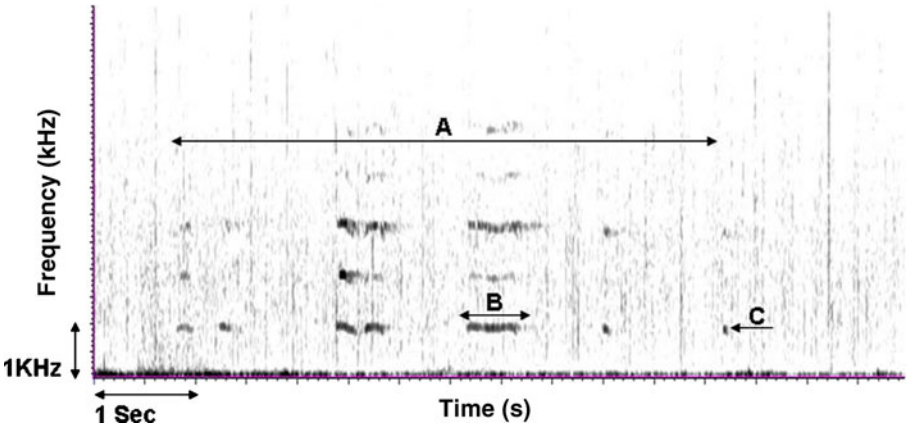

Fig. 1 Example time-frequency spectrogram of a female chimpanzee copulation calling bout from the Budongo Forest, Uganda. Filter bandwidth: 159 Hz, frequency resolution: 86.1 Hz. Copulation calling bouts (**a**) are composed of a number of individual copulation calls (**b**). In addition, *C* indicates the fundamental frequency of the call.

as the day of ovulation plus the 3 preceding days [periovulatory period (POP)], with the postovulation period being the period of maximum tumescence following POP.

Acoustic Analyses

We recorded copulation calls with a SENNHEISER ME66 directional microphone and MARANTZ PMD660 solid-state recorder. We conducted quantitative call analysis with PRAAT version 4.3.17 using an automated script written by M. Owren. We focused on the following temporal parameters: 1) call bout length (s): total duration of the copulation calling bout, 2) *N* call units: number of individually distinct call units within the calling bout, and 3) intercall interval (s): time duration between each successive call unit. The following frequency measurements were taken: 1) peak fundamental frequency: location in the frequency domain where maximum acoustic energy occurred in the F0 in the call middle (Hz); 2) peak frequency at call beginning: frequency at which maximum acoustic energy occurs at call beginning (Hz); 3) peak frequency of the call at call middle: frequency at which maximum acoustic energy occurs at call middle (Hz); 4) peak frequency of the call at call end: frequency at which maximum acoustic energy occurs at call end (Hz); 5) transition onset: frequency modulation between call beginning and middle (Hz); 6) transition offset: frequency modulation between call middle and call end (Hz); 7) mean fundamental frequency: average frequency in the fundamental band over the whole call unit (Hz).

Statistical Analyses

We analyzed all calls given during a copulation calling bout and calculated a median value for each parameter, which we then subjected to statistical analyses. To investigate whether females provided reliable information about their fertility states, we compared the acoustic structure of copulation calls between the fertile POP (N_{calls}=16) and the nonfertile, post-POP (N_{calls}=10) from 5 complete maximally tumescent oestrus cycles (LL: *N*=1; NB: *N*=2; WL: *N*=2). To determine if female chimpanzees gave individually distinctive copulation calls, we analyzed 256 individual calls (constituting 71 calling bouts) from 6 cycling females (LL: *N*=23; MK: *N*=11; NB: *N*=9; WL: *N*=19, JL: *N*=4; KY: *N*=5). We ran MANOVAs and 2-way univariate GLMs to explore the effects of the categorical variables, identity and cycle stage, respectively, on the acoustic structure of copulation calls. Univariate GLMs account for multiple contributions from the same individual by incorporating female ID as a random factor in the model (Pinheiro and Bates 2000). To test further whether acoustic structure could be assigned to the identity and cycle stage, we performed a discriminant function analysis (DFA). Because cycle stage was confounded by multiple contributions from the same female, we conducted a permutated discriminant function analysis (pDFA) using scripts provided by R. Mundry (Mundry and Sommer 2007). We performed colinearity checks for the 10 parameters and found that all had satisfactory variance inflation factors of <7.0 (Allison 1999; Slocombe and Zuberbühler 2007). We conducted all tests using SPSS

version 15.0 and R version 2.8.1 (R core development team, www.R-Cran.org). We set α=0.05.

Results

Female Ovulatory Status

A 2-way between-subjects ANOVA (with female identity as a random factor) indicated that the female's fertile phase had no effect on any of the 10 temporal or spectral acoustic parameters (Table I), suggesting that the transition from fertile to nonfertile was not acoustically marked in chimpanzee copulation calls. Unsurprisingly, a pDFA did not discriminate between calls based on cycle stage, with cross validation analysis correctly classifying only 8/1000 cases (p value for cross validation=0.12)

Female Identity

A between-subjects MANOVA on the median values showed that female identity significantly affected the acoustic structure of copulation calls (F(5,60)=2.288, Wilks' λ=0.47, p<0.001). Five of the 10 acoustic parameters varied significantly among individuals irrespective of cycle stage (Table II). The acoustic parameters that accounted for most of the variance were all frequency measures: peak frequency in F0 (F(5,42)=7.350, p<0.001, peak frequency at call beginning (F(5,42)=3.176, p=0.016), peak frequency at call end (F(5,42)=3.808, p=0.006), transition onset (F(5,42)=4.431, p=0.002), and mean pitch (F(5,42)=4.879, p=0.001). Discriminant function analysis revealed that the 10 acoustic variables explained a significant amount of variation among the individual female callers (Wilks' λ=0.085, $\chi_{(55)}^2$: 141.41, p<0.001). Calls could be classified to individual females with 56% accuracy

Table I Results of univariate ANOVAs comparing POP and post-POP for each copulation call acoustic parameter measured

Acoustic parameter	F-Value	p-Value
Call duration	$F_{1,20}$=0.139	0.74
N call units	$F_{1,20}$=0.829	0.439
Interval duration	$F_{1,14}$=0.861	0.435
Peak frequency in fundamental middle	$F_{1,20}$=0.026	0.887
Peak frequency at call beginning	$F_{1,20}$=0.154	0.73
Peak frequency at call middle	$F_{1,20}$=0.313	0.624
Peak frequency at call end	$F_{1,20}$=0.055	0.833
Transition onset	$F_{1,19}$=0.528	0.525
Transition offset	$F_{1,19}$=0.485	0.54
Mean pitch	$F_{1,18}$=0.316	0.624

Values in parentheses indicate degrees of freedom

Table II Results of a MANOVA testing in which acoustic variables contributed to the overall discrimination between female copulation calls

Acoustic parameter	*F*-Value	*p*-Value
Call duration	$F_{5,42}$=0.287	0.917
N call units	$F_{5,42}$=0.456	0.806
Interval duration	$F_{5,42}$=0.572	0.721
Peak frequency in fundamental middle	$F_{5,42}$=7.350	<0.001
Peak frequency at call beginning	$F_{5,42}$=3.176	0.016
Peak frequency at call middle	$F_{5,42}$=2.426	0.051
Peak frequency at call end	$F_{5,42}$=3.808	0.006
Transition onset	$F_{5,42}$=4.431	0.002
Transition offset	$F_{5,42}$=0.478	0.791
Mean pitch	$F_{5,42}$=4.879	0.001

Values in parentheses indicate degrees of freedom

(cross-validated), a rate significantly above chance expectation (binomial (0.167), $p<0.001$, 2-tailed).

Discussion

Results from our acoustic analysis of female chimpanzee copulation calls suggest that these vocalizations do not appear to encode information regarding the ovulatory status of females when comparing calls recorded during fertile and nonfertile periods, but are individually distinctive. The findings are in line with previous studies focusing on the information content of primate copulation calls (Pfefferle *et al.* 2008; Semple 2001), but ours is the first systematic study to address this question in apes.

In a previous study, we proposed that female chimpanzees use copulation calls in flexible ways, possibly to confuse paternity and to gain the future support of adult community males (Townsend *et al.* 2008). However, this hypothesis was based purely on call use, i.e., the contexts in which these calls were produced. Results from the present study are consistent with the paternity confusion hypothesis because copulation call structure does not appear to vary from fertile to nonfertile periods. Although chimpanzee females appear to be generally motivated to advertise their receptive state through calling, they do not provide accurate information about the timing of ovulation, a pattern also found in Barbary macaques (Pfefferle *et al.* 2008). By concealing ovulation, females may prevent monopolization by a socially dominant male and thereby increase paternity confusion (Pradhan and van Schaik 2008), a strategy that is likely to secure them future protective support by multiple males. We here managed to observe a number of adult females in their natural habitats under difficult observation conditions. Nevertheless, the resulting sample size was small and, as always, it is difficult to draw firm conclusions from negative evidence. In this sense, our results should be treated with caution until additional

work from other chimpanzee communities, which also incorporates more balanced data in addition to pre-POP and POP vocalizations, is performed.

Of course male primates may use other cues to assess the proximity to ovulation. One potential signal is, e.g., the swelling size (Bielert and Van der Walt 1982; Deschner *et al.* 2003, 2004; Higham *et al.* 2008). In chimpanzees, specifically, there seems to be some relationship between perineal swelling size and proximity to ovulation; however, these discrete changes do not provide enough information to deduce its exact timing, thereby allowing some room for paternity confusion and alpha male monopolization prevention (Deschner *et al.* 2003). Not signaling ovulation vocally may, to an extent, help to complement the inaccurate information provided by the swelling (Semple 2001).

Chimpanzee males exhibit mating preferences for older females (Muller *et al.* 2006), possibly because they require fewer cycles before conception (Deschner and Boesch 2007). Given that concurrently cycling estrous females may compete with each other over access to males (Pfefferle *et al.* 2008; Townsend *et al.* 2008), the ability to convey identity becomes a useful tool, keeping potential listening male mating partners informed as to the whereabouts of certain females. Further, signaling identity provides additional information on the number of copulations in which a female has engaged, information that is absent from the visually based sexual swelling (Semple 2001). Although it is true that most animal vocalizations are likely to vary between individuals (Tibbetts and Dale 2007), including copulation calls (Semple 2001), a considerable amount of empirical testing of this assumption is yet to be performed. For example, the copulation calls of yellow baboons have previously been shown to encode individual identity, and males appear to attend to this information, discriminating between individuals (Semple 2001), yet the exact mechanisms underlying discrimination still remain unclear. For chimpanzees, however, individual signatures in copulation calls may play an even more critical role in guiding future behavioral decisions of community males than in terrestrial monkey species. Because of their fission–fusion social system, female chimpanzees can spend long periods of time out of contact with males, associating only with other females or family units (Goodall 1986; Reynolds 2005). This may make it difficult for males to track the sexual progression and behavior of females, in comparison to other primate species also using copulation calls, e.g., Barbary macaques and yellow baboons, in which males and females reside together as a cohesive group in open, highly visual habitats and hence the following of certain females and their corresponding sexual behavior is logistically easier.

Taken together, our results suggest that one potential function of chimpanzee copulation calls is to spread the probability of paternity more evenly among adult male group members. Acoustically, copulation calls can be assigned to individual females. Labeling one's own identity may increase fitness when multiple females are cycling, and concealing the transfer from fertile to nonfertile periods may help to prevent monopolization and paternity concentration. From this, a next step will be to elucidate what additional information sets are encoded within copulation calls and of course to verify experimentally whether male or indeed female receivers are guided in their natural behavior by these differences, or lack thereof, we have so far detected. Such experimental work is crucial for verifying behavioral patterns elucidated and for further understanding whether information encoded in vocal-

isations—possibly the most crucial communicative medium in the wild—is meaningful at some level to chimpanzees.

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